Biology of a New *Trypoxylon* that Utilizes Nests of *Microstigmus* in Costa Rica (Hymenoptera: Sphecidae)

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In the Neotropics, spider-hunting wasps of the genus *Trypoxylon* are extraordinarily diverse (Bohart and Menke, 1976). The subject of this report was first noted in 1968 (Matthews, 1968:37), but no adults were collected until 1980. Professor O. W. Richards and Dr. Arnold S. Menke kindly examined the wasp, declared it to be a new species, and very graciously offered to describe it. My notes on nesting biology follow the species description.

Trypoxylon latro Menke & Richards, NEW SPECIES (Figs. 1–13)

Holotype male.—Color: Black. Scape, pedicel pale brown above, whitish yellow below; clypeal margin, labrum and mandible pale brown; palpi, pronotal lobe, precoxal lobes, coxae apically, trochanters and foretarsus pale yellow; forefemur brownish above, brownish yellow below; midfemur brownish; fore and midtibiae brownish yellow; midtibial spur and basal half of tarsomere I pale yellow, rest of midtarsus brownish; basal third of hindtibia and spurs pale yellow; hindtarsus brownish.

Vestiture: Clypeus and lower frons, including eye emarginations, with dense appressed silver setae; gena, pronotal collar, scutum laterally, metanotum laterally, mesopleuron, propodeal dorsum and hindface with sparser, suberect silver setae; rest of body covered with fine, pale setae except metapleuron and propodeal side glabrous.

Structure: Flagellomere VIII abruptly expanded apically in profile, IX-XI of same width (Fig. 13); flagellomeres III-IV and VII-VIII with narrow polished tyli (those on III–IV very difficult to detect even at $75\times$); flagellomere IV flattened and with small apical tooth-like process; comparative lengths of flagellomeres I-II and XI: 7:5.5:17; greatest length of flagellomere XI slightly more than combined lengths of VIII-X; frontal carina evanescent, represented by short, polished line above transverse supra-antennal carina; frons minutely granulate, dull, shallowly punctate, punctures separated by about two diameters; least interocular distance at vertex nearly twice that at clypeus (21:12); ratio of ocellocular distance to hindocellus diameter to distance between hindocelli: 2:6:4.5; clypeal free margin as in Fig. 2, edge thickened at middle third as seen from below; labrum consisting of two narrow, fingerlike lobes; occipital carina a complete circle, separated from hypostomal carina by slightly less than a hindocellus diameter (4.5:6); scutal and scutellar sculpture and punctation similar to from but weakly shining; propodeal dorsum with pair of shallow, arcuate furrows which are evanescent posterad, resulting enclosure with broad, shallow, median longitudinal depression which is cross carinulate, carinae strongest and converging at base of enclosure; propodeal

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side highly polished, impunctate except for zone of dense setae posteriorly above hindcoxa, side delimited dorsad by arcuate shelf-like ridge, dorsal rim of petiole socket without a backward projecting lamella; posterolateral corner of propleuron with roughly egg-shaped platelike area which is delimited inwardly by a carina; mesopleuron finely, shallowly⁻punctate, depression around scrobe about equal to hindocellus diameter; metapleuron highly polished, impunctate except above hindcoxa; metapleural flange lamellate, its margin translucent, not down curved; intercoxal carina slightly arcuate; dorsal carina of hindcoxa not reaching coxal apex; gaster claviform, segment I gradually expanding toward II, I not quite twice as long as wide (46:28) in dorsal view; sternum VIII as in Fig. 8; genitalia as in Fig. 11, aedeagal shaft arcuate in lateral profile, penis valve head with sharp lateral process.

Length: 6 mm.

Female.—Color: As in male except scape yellow brown, pedicel brown above, yellow brown beneath; foreleg whitish yellow except upper surface of femur with brownish stripe and coxa yellowish brown; midfemur brownish but with pale yellow area at base; midtibia pale yellow behind, basal fourth of gastral segments II–III ringed by pale yellow.

Vestiture: Same as male.

Structure: As in male except: flagellum simple, comparative lengths of flagellomeres I–II and X: 13.5:11:15.5; flagellomere X length equal to combined lengths of VIII–IX; least interocular distance at vertex more than twice that at clypeus: 23.5:10.5; ratio of ocellocular distance to hindocellus diameter to distance between hindocelli: 1.5:7.5; clypeal margin less sinuate than male (Fig. 5); inner margin of mandible simple as in male (Fig. 5); length of tergum I a little less than twice width (range: 58:35–55:32).

Length: 6-6.5 mm.

Discussion.—The clavate gaster of *T. latro* is suggestive of the monotypic genus *Pisoxylon* Menke (1968), and both have a bilobed labrum and somewhat similar male antennae. But *Pisoxylon* has a much more compact gaster, the occipital carina runs into the hypostomal carina, the propodeal side curves to the dorsum without interruption, the metapleural flange is not lamellate, the hindcoxa has only a suggestion of a dorsal carina, sternum VIII is roundly acuminate, the gonostyle is not bilobate and the penis valve lacks spines or other processes. In T. latro the occipital carina is a complete circle which is separated from the hypostomal carina, the propodeal side is highly polished, glabrous, and sharply delimited dorsally by a shelf-like ridge, the metapleural flange is broadly lamellate, the hindcoxal carina is strongly indicated, male sternum VIII is truncate apically and bispinose, the gonostyle is bilobed and the penis valve is adorned with spinose processes. These characters negate a close relationship with *P. xanthosoma*, and they indicate that T. latro belongs in the fabricator group (see Bohart and Menke, 1976:344, and Richards, 1934:280) of Trypoxylon. In fact, latro is very similar to the North American species T. johnsoni Fox and T. clarkei Krombein as demonstrated by the labrum, the male antenna, sternum VIII, the male genitalia and the general habitus.

T. latro differs from *johnsoni* in the following ways: In both species the propodeal side just above the hindcoxa is densely covered by setae which rather sharply delimit this zone from the remainder of the side. In *johnsoni* a ridge

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Figs. 1–12. Details of *Trypoxylon* species. 1–3, male clypeus and mandible. 4–6, female clypeus and mandible. 7–9, male sternum VIII. 10–12, ventral view of male genitalia.

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Fig. 13. Two views of left male flagellum of Trypoxylon latro.

extends dorsad from the hindcoxal articulation partially delimiting this setal zone. This ridge is usually paralleled anterad by several shorter ridges. The least interocular distance is comparatively shorter in females of *latro*. When the interocular distance at the vertex is compared to that at the clypeus and the length of flagellomere I the resulting ratios are obtained: latro: 23.5:10.5:13.5, johnsoni: 26: 18:16. The female clypeus of *latro* (Fig. 5) lacks the two prominent, rounded lobes (Fig. 4) found in *johnsoni*. The inner margin of the female mandible is simple in latro (Fig. 5), but there is a weak tooth in *johnsoni* (Fig. 4). In both sexes of *latro* the hindocelli are separated by less than an ocellus diameter (5:7.5), while in johnsoni they are separated by an ocellus diameter or more (7:7). The male antennae are quite similar in the two species, but flagellomere VIII of johnsoni lacks a tyloid. Furthermore, flagellomere IV in johnsoni has a semicircular depression which accentuates the apical toothlike process. Tergum I in *latro* is about twice as long as wide or slightly less in the female, while in *johnsoni* it is almost three times as long as wide. In the male of *latro* I is less than twice as long as wide, while in *johnsoni* it is slightly more than twice as long as wide. The male genitalia are very different (compare Figs. 10, 11). In *latro* the gonostyle ends in two elongate, broad flat lobes which overlay each other dorsoventrally (Fig. 11). In *johnsoni* the gonostyle ends in two narrow lobes which lie side by side, the outermost being narrower and attenuate apically (Fig. 10).

T. latro is immediately separable from *clarkei* by the complete occipital carina. In *clarkei* the carina is incomplete below, although the gap between the ends is narrow in some males. The propodeal side of *clarkei* is less densely setose posteriorly above the hindcoxa than in *latro*, and the shelf-like dorsal ridge is weaker, but these are features that require specimens of both species to appreciate. The intercoxal carina is straight in *clarkei*, arcuate in *latro*. In the female of *clarkei* the least interocular distance at the vertex is about twice that at the clypeus, the distance at the latter equalling the length of flagellomere I (29:14:14). In *latro* the ratios are 23.5:10.5:13.5. The female clypeus of *clarkei* is produced into a truncate lobe, and there is a weak tooth on the inner margin of the mandible (Fig. 6). In both sexes of *clarkei* the ocellocular distance is equal to half (female) or two-thirds (male) a hindocellus diameter. In both sexes of *latro* the ocellocular distance is less than half a hindocellus diameter. As in *latro*, the apical lobes of the gonostyle of *clarkei* are broad and overlay each other, but ventrally there is a dense "basket" of long curved setae at their base (Fig. 12, also illustrated by Sandhouse, 1940: Fig. 48—misidentified as *johnsoni*). The gonostyle of *latro* lacks the basal "basket" and is sparsely setose in general (Fig. 11).

Etymology.—*Latro* is a Latin noun meaning robber which refers to the habit of using nests of *Microstigmus* for its own.

Types. – Holotype &: COSTA RICA, Puntarenas Prov., Corcovado Natl. Park, Sirena Station, nest 71, March 8, 1981, R. W. Matthews (USNM type #100374). Paratypes: 4 &, 10 \circ , same place as type, various dates in February and March 1981, and Oct. 1980, all R. W. Matthews or Matthews and C. K. Starr, deposited in U.S. National Museum, British Museum (Natural History), Univ. of Georgia, Univ. of Costa Rica, and Univ. of Sao Paulo.

BIOLOGICAL NOTES

Study method. – This study was conducted between October 1980 and September 1982 at Sirena, in Corcovado National Park on the Osa Peninsula, Guanacaste Province, Costa Rica. In the primary forests along the Ollas Trail, the eusocial sphecid wasp *Microstigmus comes* nests abundantly on the palm *Crysophila guagara*. Monthly censuses of all *M. comes* nests in the study site were taken, so that complete records of individual nest histories were obtained for over 700 nests, many of which were appropriated by *T. latro* (Fig. 14). *Trypoxylon latro* nests were collected during 4 extended visits to the study site. Dissections of these nests, rearings, and incidental observations produced the information reported here.

Nest architecture. – Trypoxylon latro utilizes only the empty upper portion or "attic" of the *M. comes* nest. There appears to be no modification of existing *M. comes* cells or the nest entrance other than the application of irregular splotches of mud to the floor and sides of the nest interior. I could find no trace of old *M. comes* cells or their contents. Petioles of nests appropriated by *Trypoxylon* often lose their distinctive tight coil and become "wavy" (Fig. 14), a useful field cue. Presumably this loss of coil tightness reflects a lack of the maintenance normally given by *Microstigmus* adults, rather than modification by *T. latro* females.

Dissections of 86 nests from 4 collections are summarized in Table 1. Nests contained an average of 1.3 cells (range 1–3). There was a marked seasonal difference in the average nest size. Nests constructed in the wet season (August–October) averaged 1.19 cells (n = 57), whereas those constructed in the dry season (February–March) were larger, averaging 1.62 cells (n = 21). This difference is highly significant (Mann-Whitney Test, z = 3.56, P < 0.0002). Similarly, the number of nests with 2 cells was significantly greater in the dry season ($\chi^2 = 9.64$, P < 0.01). When 2 cells were constructed, a weak mud partition of about 0.5 mm thickness separated the lower (first-made) cell from the upper one. Due to the pear-like shape of an *M. comes* nest, the upper cell was invariably smaller in size and volume. In the single nest with 3 cells, the lower space was partitioned in half. Empty "vestibule" cells between the upper cell and the sealed nest entrance



Fig. 14. A *Trypoxylon latro* female carrying prey into the entrance of a *Microstigmus comes* nest. Constructed of the waxy pubescence found on the underside of *Crysophila guagara* palms and bound together with silk, the nest now lacks the strong petiole coil characteristic of an active *Microstigmus* colony (cf. Fig. 4 in Matthews, 1968). The petiole is about 14 mm long.

occurred in 7% of all nests, all from the wet season. Four nests had a final closure but were entirely empty.

Life history.—The egg, about 1.2 mm long and 0.4 mm wide, was attached obliquely to the anterior lateral surface of the spider's abdomen. Two eggs observed in the laboratory hatched within 3 days of collection.

Larval growth was rapid. In the single case observed, a newly hatched larva completed its full growth and constructed a cocoon in 4 days. Such rapid devel-

Collection date	Nests in sample	Nests without cells			Nests with cells							
		Mud- líned only	Empty but with final closure	Total cells/nest			Vesti-	Provisioning			Coccoon	
				1	2	3	cell present	Incom- plete	Scav- enged	Egg	Un- emerged	Emerged
October 1980 Feb.–March	23	0	1	13	8	1	3	1	8	2	5	12
1981 September	24	2	1	8	13	0	0	1	0	0	20	14
1981 August 1982	7 32	0 2	0 2	6 25	1 3	0 0	0 3	0 0	2 101	2 3	1 8	3 7

Table 1. Contents of 86 *Trypoxylon latro* nests from 4 collections (1 dry season, 3 wet seasons) taken at Sirena, Corcovado National Park, Costa Rica.

¹ Three individuals of an unidentified chloropid fly were reared from 2 nests.

opment may explain the absence of nests with larvae among those summarized in Table 1.

Rounded at both ends, cocoons were attached basally to a bit of the mud in the cell bottom and stood upright or obliquely in the cell (Fig. 15A). Dull gray and of a grainy and brittle texture, cocoons measured an average of 6.8 mm long (range 5.3-7.5, n = 20) and 2.1 mm wide (range 1.8-2.3, n = 20). Four female cocoons averaged 7.0 mm long (range 6.3-7.5) and a single male cocoon was 6.5 mm long. Overall, cocoons from nests with 2 cells averaged slightly smaller than those from single-celled nests, for those from the upper cells were all at the small end of the size range.

Duration of the pupal stage could not be precisely documented, but eclosions from collected nests continued over a period of at least 2 months. No diapause or quiescent stage was detected.

Overall the sex ratio of the reared adults was 18 females to 8 males. However, emergences from the 14 single-celled nests were strongly female-biased (11 females: 3 males). Five of the 6 two-celled nests from which both adults emerged yielded one of each sex. Presumably the males came from the smaller cocoons of the upper cells. Upon emergence, adults characteristically chewed directly through the side wall of the nest bag rather than through the mud closure plug.

Prey.—Cells were mass provisioned with spiders (Fig. 15B). A sample of 133 spiders from 8 cells was preserved. The number of prey per cell averaged 16.6 (range 9–28). Dr. H. W. Levi of the Museum of Comparative Zoology, Harvard University, identified them as *Leucauge* and *Dolichognatha* in the Tetragnathidae. *Leucauge* was uncommon in the sample, with only 6 juveniles represented. However, at least 2 species of *Dolichognatha* were represented. Nearly half (48%) of the individuals were juveniles, 13.7% were males, and 38.3% were females. According to Dr. Levi, *Dolichognatha* constructs small orb webs at the base of trees. Neotropical tetragnathids are largely unstudied, but recent revisions of Nearctic genera are available (Levi, 1980, 1981).

Natural enemies.—As shown in Table 1, nest cells attacked by scavenger fly larvae were found in all 3 wet season collections but not in the dry season collection. In the wet season 12.5–32.1% of total cells were infested. In August 1982, 3 unidentified chloropid fly adults were successfully reared from scavenged prey

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Figs. 15A, B. A, cocoon of T. *latro* attached by its posterior end to a spot of mud in the bottom of the nest. Cocoon is 7.0 mm long. B, *Dolichognatha* spider prey and small larva of T. *latro* in an M. comes nest.

in 2 nests. An unidentified ichneumonid wasp was reported as emerging from a cocoon in a mud-plugged nest in 1968 from a different locality (Matthews, 1968), but none were taken in the present study.

Adult behavior.-On 7 March 1981, a female was observed carrying prey into

an M. comes nest in which, 6 days earlier, a single M. comes female had been present. The nest was less than 4 weeks old according to census records. Whether T. latro usurped the nest or took over after it had become abandoned is undetermined, but the evidence suggests that the nest may have been usurped.

Provisioning was first noted at 1110 AM CST when the female *T. latro* was seen to enter with prey. During the next 116 minutes she brought in 10 additional spiders. Time away from the nest ranged 3-42 minutes (n = 10), whereas the time inside the nest to store the prey was always brief, ranging 5-18 seconds. After a lapse of 81 minutes I returned to the nest at 1645 PM. The female returned with a spider at 1647, and remained inside for 49 seconds before departing. Presumably oviposition occurred at this time, for 2 minutes later she returned carrying mud, then made 5 more trips for mud in rapid succession, each requiring less than 1 minute. All of this mud was applied inside the nest, with the wasp spending 46-70 seconds each time at this task. During these periods of mud application I was unable to detect any audible buzz like that produced by the subgenus *Trypargilum* during mud application. Presumably the wasp was closing off the lower cell at this time.

Impact on host population.—At my study site, monthly census of the status of all M. comes nests from February, 1981 to May, 1982 revealed that T. latro utilized a relatively small but more or less constant proportion of about 5% of the potentially available nests. The average number that became Trypoxylon nests each month was 9.8 (range 5–21) of an average of 187 active M. comes nests.

Two other Sirena samples of nests from outside of the census area gave comparable rates of *T. latro* nest utilization. The first involved 64 *M. comes* nests collected at night on 8 March 1981 (dry season). Five (7.8%) proved to be occupied by *Trypoxylon*. A second night-collected sample, made on 4 September 1982 (wet season), involved 65 nests, of which 6 (9.2%) were *Trypoxylon*. Of these, 4 were in nests known to be constructed by *M. comes* more than 3 months earlier, and 2 were in nests constructed within the past 3 months. According to the nest census records from the study site, nests of all ages are vulnerable to appropriation by *T. latro*. No preference for nests of a particular age could be detected. Overall, activity of *T. latro* accounted for 24% of the total *M. comes* mortality in the study site.

Discussion. – Trypoxylon is a huge genus with over 450 species and a great diversity of behavior. It includes two subgenera, Trypoxylon and Trypargilum. The revision of the American Trypoxylon by Richards (1934) remains the definitive study of the genus in the New World. Coville's (1982) revision of the subgenus Trypargilum in North America is a recent contribution to the taxonomy of that group. The widespread use of preformed cavities for nesting, including the abandoned cells of other wasps, has allowed researchers to use the trap-nest technique (Coville and Coville, 1980; Coville, 1981; Coville and Griswold, in prep.) to expand our knowledge of Neotropical Trypargilum. Species of the subgenus Trypoxylon are less well known, and probably many undescribed species exist. Many also take trap-nests and at least 2 species, T. johnsoni and T. clarkei, characteristically nest in preexisting cavities (Krombein, 1967). However, members of the fabricator group, to which T. latro, johnsoni, and clarkei belong, typically construct free mud nests.

The use of Microstigmus nests by T. latro is unique. Building a mud nest within

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the small, flexible silk-lined nest sacs of these primitively social wasps would seem rather analogous to building a house inside a laundry bag. Moreover, abandoned nest sacs are rather delicate and rarely persist for long before the petiole breaks or becomes detached from the plant leaf.

In the Neotropics, insects, particularly ants, compete intensely for cavities suitable for nesting. Ants have exploited a great variety of seemingly unlikely cavities, from hollow thorns to galls. Virtually every hollow twig that one breaks open is occupied by ants. The vast majority of trap-nests that I have placed in the field in various localities in Costa Rica have been quickly exploited by ants. However, of over 700 *Microstigmus* nests monitored over a 16 month period, only one was found to be occupied by an ant colony (a species of *Tapinoma*). Thus, *Microstigmus* nest bags are apparently either being overlooked by searching ants or are in some manner unacceptable to them. By exploiting this unusual habitat, *T. latro* minimizes competition from ants. Furthermore, since no parasites were reared from any nests in this study, *T. latro* also appears to be avoiding certain other sources of mortality, such as chrysidid wasps, that regularly parasitize related species nesting in more "typical" habitats.

Yet despite the abundance of potential nest sites, *T. latro* is a relatively rare species. Due to the small size of the *Microstigmus* nest bag, nests rarely contain more than 2 cells. While *T. latro* nests continuously throughout the year, it clearly is more successful during the dry season. Dry season nests contained significantly more cells and suffered no losses to scavenger flies. These differences probably reflect differences in prey abundance, humidity, and available time for nesting.

Trypoxylon latro is unusual in that its brittle grainy cocoons are unlike "typical" *Trypoxylon* cocoons, which are papery and tan-colored. However, at least one other *Trypoxylon* species, *T. johnsoni*, constructs a similar cocoon and also nests in preformed cavities (Krombein, 1967). As Menke and Richards note in their description, *T. latro* is closely related to *T. johnsoni* morphologically. Dr. Krombein kindly loaned me cocoons of *T. johnsoni* for comparison and they are virtually identical to those of *T. latro*, which is additional evidence for the close relationship of these 2 species.

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